TROPHIC AND MICROHABITAT NICHE OVERLAP IN TWO SYMPATRIC DENDROBATIDS FROM LA SELVA, COSTA RICA

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Resumen. — Se estudio la ecología trófica y uso del microhábitat de *Dendrobates auratus* y *Oophaga pumilio* en un área de simpatría entre las dos especies ubicada en la Estación Biológica La Selva, Costa Rica. En este sitio ambos dendrobatidos son simpátricos debido a la introducción y naturalización de *D. auratus* en los últimos 24 años. La dieta de ambas especies se describió a partir del análisis de la técnica del lavado de estómago. Los microhábitas utilizados fueron definidos según el sitio donde cada ejemplar fue capturado. La relación en el uso del microhábitat y la ecología trófica entre ambas especies fue evaluada utilizando el índice de solpamiento de Pianka (Ojk) en el análisis de la dieta (proporción de presas y volumen) y en el uso del microhábitat. La dieta de ambos dendrobátidos estuvo caracterizada principalmente por el consumo de himenópteros (hormigas), ácaros, y colémbolos, resultando consecuentemente en un alto índice de solapamiento en la proporción y volumen de las presas, sin embargo, este alto solapamiento no fue significativo y no implicó la presencia de interacciones negativas entre ambas especies. El uso del microhábitat presentó un solapamiento muy bajo y no significativo, indicando una diferenciación en los microhábitats utilizados por cada especie. La ausencia de interacciones negativas en cuanto al uso de los recursos tróficos entre ambos dendrobátidos podría deberse a la diferenciación en el uso del microhábitat, y posiblemente, a la abundancia de presas en el área. El gran volumen de formícidos y ácaros en la dieta de estas dos especies son consistentes con la hipótesis del consumo de estos artrópodos como una fuente de alcaloides.

Palabras clave: *Dendrobates auratus*, *Oophaga pumilio*, dieta, microhabitats, complementariedad.

Abstract. — We studied the trophic ecology of *Dendrobates auratus* and *Oophaga pumilio* in La Selva Biological Station, Costa Rica. At this site, both dendrobatids are sympatric due to the introduction and naturalization of *D. auratus* in the last 24 years. Diets of both dendrobatids were recorded by the analysed stomach flushing technique. Microhabitats uses were defined as the site where each individual was captured. The influence of microhabitat on diets was evaluated by the dietary (prey proportions and volume) and microhabitat overlaps using Pianka's (O_{jk}) overlap index calculated with EcoSim software. Diets of both dendrobatids were principally characterized by the preference of hymenopterans (ants), acarines and collembolans, resulted in a high overlapping in prey proportions and prey volume. However, diets overlaps were not significant, suggesting the absence of negative feeding interactions. Microhabitat use was low overlapped and also not significant, suggesting a differentiation on the use of spatial resource. The absence of negative feeding interactions between *Dendrobates auratus* and *Oophaga pumilio* could be due to segregation in microhabitat use and possible by the abundance of trophic resource in the area. The great large volumes of formicids and acarines in the diet of this dendrobatids are in agreement with the hypothesis of these arthropods as a dietary source of alkaloids.

Keywords: *Dendrobates auratus*, *Oophaga pumilio*, diets, microhabitats, complementarity.

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INTRODUCTION

The differential utilization of resources provides essential information to understand the role of individual species in communities and has been indicated as the key would allow the coexistence between sympatric species (Schoener, 1974; Toft, 1981; Lieberman, 1986; Duré and Kehr, 2004). Several studies conducted in sympatric anurans species, showed that some differences in food resource use may be caused by different foraging patterns, microhabitat use, seasonal and daily activity, and resource availability (Toft, 1980a; Toft 1980b; Toft 1985; Graves, 1999; Almeida-Gómez *et al*., 2007; Cuevas and Martori, 2007; Duré *et al*., 2009). Within the limitations imposed by evolutionary history, exploitation of particular prey by a species can influence the interactions of that species in a particular environment and, hence, may determine activity periods, reproductive features, and predator–prey interactions (Polis *et al*., 1989; Caldwell, 1996)

Dendrobates aurautus and *O. pumilio* (Anura; Dendrobatidae) are two common leaf litter dendrobatids species which inhabit the wet tropical and subtropical forest of down lands in Central America and North of South America, being sympatric at many sites in Costa Rica, Nicaragua and Panamá (Savage, 2002). Both dendrobatids are listed as Least Concern by IUCN (Solis *et al*., 2008a,b) because they are tolerant to a certain degree of habitat modification and their populations appears to be large. The main threats to these species are habitat loss and over-collection for pet trade. The bright coloration and diurnal activity of *D. auratus* and *O. pumilio* make these frogs conspicuous and very attractive, playing an important role in attracting tourist along its distribution. In consequence, *D. auratus* has been introduced in various localities to increase tourism in Costa Rica in recent times. For example, the establishment and naturalization of *D. auratus* at La Selva, is quite recent (within the last 20 years) and due to the introduction of this species by a local employee of a tourist lodge in the near locality of Chilamate in 1986 (Guyer and Donnelly 2005). However, despite the naturalization of *D. auratus* at La Selva, its distribution at this site is restricted only along the margins of Tres Rios path (R. Cajade, pers. obs).

Single studies conducted in *D. aurautus* and *O. pumilio* determined that these dendrobatids are closely related in diet, reproduction and habitat preference (Toft, 1981; Lieberman, 1986; Pough and Taigen, 1990; Donnelly, 1991). Diet, diurnal activity and aposematic coloration of both dendrobatids are involved in an evolutionary process of chemical defense implicating skin toxins, mainly alkaloids (Caldwell, 1996; Santos *et al*., 2003; Saporito *et al*., 2003; Darst *et al*., 2005; Saporito *et al*., 2009).While *D. auratus* and *O. pumilio* are probably the dendrobatids most extensively studies (Caldwell, 1996; Graves, 1999), their feeding ecology and microhabitat use have not been analyzed in sympatry.

The aim of this study is describe the trophic ecology and microhabitat use of *D. auratus* and *O. pumilio* in a secondary forest from La Selva, Costa Rica, where these species occurs in a condition of no natural sympatry.

MATERIALS AND METHODS

Field work was carried out during dry season between 2-17 March, 2008, in a plot of secondary forest located in the biological station La Selva, Costa Rica. Individuals of *D. auratus* and *O. pumilio* were captured by hand at 7:00 and 18:00 hs, along the margins of Tres Rios path between 1200 and 2900 m. of the trailhead (Fig. 1). Immediately stomach contents of each frog were flushed (see Sole *et al*., 2005 methodology) and

fixed in 5% ethanol to identify prey in laboratory. This technique allowed us obtaining stomach contents quickly without sacrificing the frog, and avoiding the loss of samples by reducing the digestion time occurred since the collection until obtaining its stomach contents (Sole *et al.*, 2005). Body length (mm) and mouth width (mm) were measured for each individual with calipers to nearest 0.01 mm. Each individual was identified for its dorsal and ventral pattern registered by a digital photograph to avoid pseudo-replication. Prey items were identified to order (following Borror and White, 1970) except ants that were identified to family and considered as a separate item prey. All measurements were made using an ocular micrometer to the nearest 0.01 mm under a stereomicroscope. Microhabitat categories recorded for each individual frog were: (1) wet ground covered with ferns, (2) leaf litter associated with the base of cacao plants and trees, (3) anthills, and (4) under fallen tree trunks. The number of prey items per stomach for each prey category was recorded. Volume of each prey item was estimated using the formula for an ellipsoid,

$$V = 4/3\pi\ (1/2L)\ (1/2A)^2$$

where V is volume, L is length and W is width (Dunham, 1983). Prey diversity was calculated used the Shannon index (H´) (Shannon and Weaver, 1949). To determine the importance of each prey category in the diet, we used the following formula:

$$I = (F\% + N\% + V\%) / 3$$

where, *F%* = occurrence percentage, *N%* = numeric percentage and *V%* = volumetric percentage (Biavati *et al.*, 2004). We calculated the importance of prey categories for pooled stomachs (IPS). The niche breadth of prey and

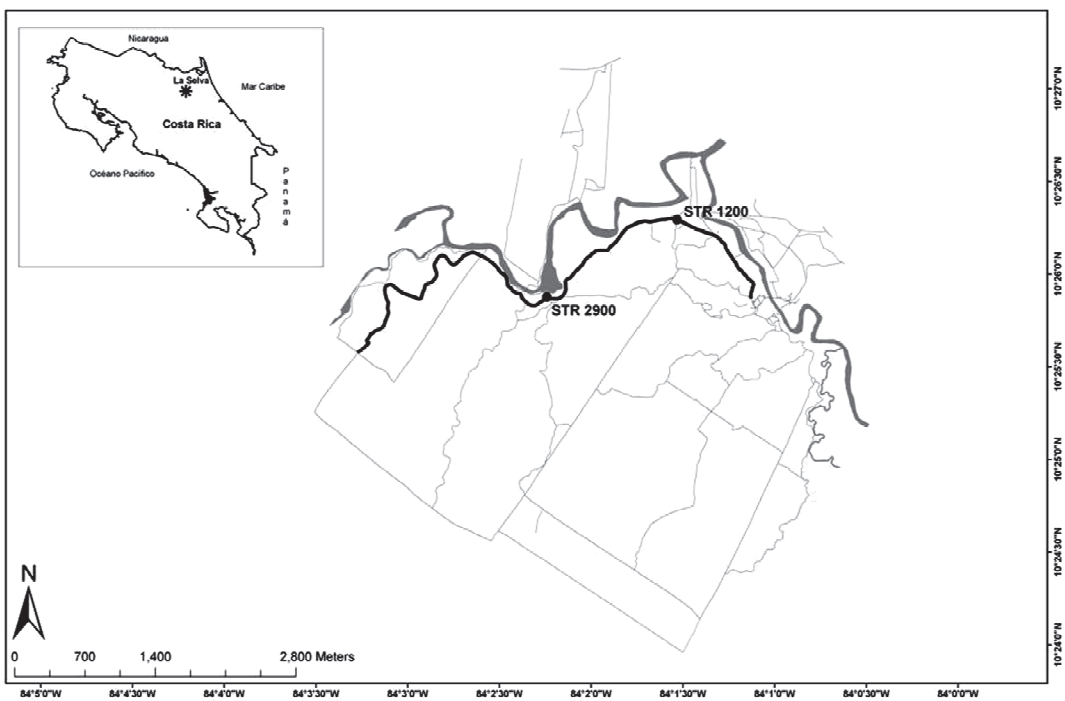

Figure 1. Detailed map of the biological station La Selva and location in Costa Rica (box). The black line represents the travel of Tres Ríos path. The study area corresponds to margins of travel between the two black points in the path.

	Dendrobates auratus							*Oophaga pumilio*						
					Frequency							Frequency		
Prey category	n	%	Volume (cm^3)	% of volume	%F	Fa	IPS	n	%	Volume (cm^3)	% of volume	%F	Fa	IPS
INSECTA														
Formicidae	746	69.01	0.3003	4.32	37	92.5	55.2	482	38.13	0.2468	4.94	35	87.5	43.5
Hymenoptera (other)	9	0.83	0.0887	1.27	8	20	7.3	15	1.18	0.0608	1.21	10	25	9.1
Homoptera	2	0.18	0.2067	2.97	2	5	2.7	2	0.15	0.0580	1.16	2	5	2.1
Diptera	9	0.83	0.4550	6.54	7	17.5	8.2	10	0.79	0.1200	2.40	5	12.5	5.2
Thyzanoptera	2	0.18	0.0506	0.72	1	2.5	1.1	2	0.15	0.0489	0.97	2	5	2.0
Collembola	64	5.92	0.0789	1.13	24	60	22.3	122	9.65	0.1272	2.54	27	67.5	26.5
Coleoptera	11	1.01	0.5347	7.69	7	17.5	8.7	14	1.10	0.7927	15.86	6	15	10.6
Hemiptera	2	0.18	0.3066	4.41	2	5	3.1	1	0.07	0.4019	8.04	1	2.5	3.5
Siphonaptera	—	—	—	—	—	—	—	1	0.07	0.0146	0.29	1	2.5	0.9
Dermaptera	1	0.09	1.0257	14.75	1	2.5	5.7	—	—	—	—	—	—	—
Zoraptera	1	0.09	1.5700	22.57	1	2.5	8.3	—	—	—	—	—	—	—
Megalloptera	—	—	—	—	—	—	—	2	0.15	0.3270	6.54	1	2.5	3.1
Larvae (Insect)	3	0.27	0.5960	8.57	3	7.5	5.4	37	2.92	0.3086	6.17	12	30	13.3
DIPLOPODA														
Polydesmida	1	0.09	0.9158	13.17	1	2.5	5.2	9	0.71	1.3310	26.63	6	15	14.1
CHELICERATA														
Acari	225	20.81	0.1068	1.53	34	85	35.7	555	43.90	0.0878	1.75	35	87.5	44.3
Araneae	—	—	—	—	—	—	—	4	0.31	0.3066	6.13	4	10	5.4
Solpugida	—	—	—	—	—	—	—	3	0.23	0.0954	1.90	3	7.5	3.2
MALACOSTRACA														
Isopoda	4	0.37	0.7169	10.31	2	5	5.2	3	0.23	0.5515	11.03	2	5	5.4
Amphipoda	—	—	—	—	—	—	—	2	0.15	0.1172	2.34	1	2.5	1.6
TOTAL	1081	100.00	6.9534	100.00	—	—	—	1264	100.00	4.9968	100.00	—	—	—

Table 1. Abundance, volume and frequency (Fa = number of stomachs containing prey item) for each prey item and importance dietary index for pooled stomachs (ISP) in the diet of *Dendrobates auratus* (n = 40) and *Oophaga pumilio* (n = 40) from La Selva, Costa Rica.

prey volume was calculated using Levins's index (Levins, 1968),

$$Nb = (\sum p_{ij}^2)^{-}$$

where p_{ij} represents the probability of finding the item i in the sample j. We calculated dietary (food proportions and volume) and microhabitat overlap using Pianka's (O_{jk}) overlap index (Pianka, 1973) using EcoSim software 7.72 (Gotelli and Entsminger, 2005) with retained niche breadth and reshuffled zero states. The EcoSim program also determines whether measured overlap values differed from what would be expected based on random sampling of the species data. EcoSim performs Mon-

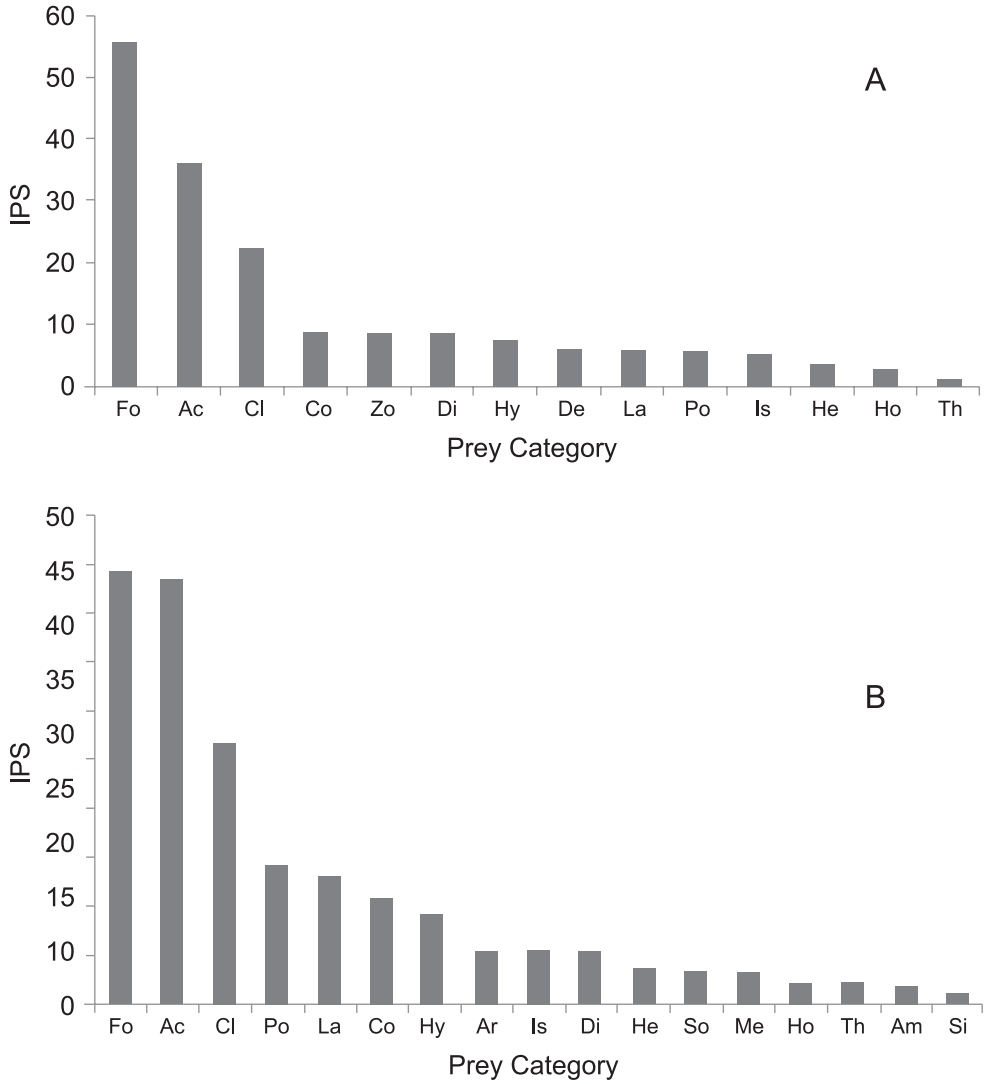

Figure 2. Importance index of prey categories ingested by *Dendrobates aurauts* (A) and *Oophaga pumilio* (B) from La Selva Biological Station, Costa Rica. IPS =importance index based on pooled stomachs. Prey categories are as follow: Ac = Acari; Am = Amphipoda; Ar = Aranae; Cl = Collembola; Co = Coleoptera; De = Dermaptera; Di = Diptera; Fo = Formicidae; He = Hemiptera; Ho = Homoptera; Hy = Hymenoptera (other than ants); Is = Isopoda; La = Larvae (Insect); Me = Megalloptera; Po = Polydesmida; Si = Siphonaptera; So = Solpugida; Th = Thysanoptera; Zo = Zoraptera.

te Carlo randomizations to create "pseudo-communities" (Pianka, 1986), and then statistically compares the patterns in these randomized communities with those in the real data matrix. In this analysis (randomization algorithms RA3; Winemiller and Pianka, 1990), "scrambled zeros", and all values of the original matrix were randomized 1000 times, and the niche breadth was retained for each species. In other words, the algorithms retained the amount of specialization for each species (Gotelli and Entsminger, 2005).

Pearson correlations coefficients (Zar, 1996) were used to establish the relationship between the morphology of predators and prey volume. When assumptions of normality were broken, the data were natural logarithms (Ln) transformed and normalized. Means were presented as mean ± standard deviation.

RESULTS

Fourteen adult specimens of each dendrobatids species were captured. All individuals had identifiable stomach contents. In *O. pumilio* were recorded three recaptures corresponding to three individuals recaptured at different sites respect to the initial capture site. Nine recaptures corresponding to three individuals were recorded in *D. auratus*: one individual recaptured six times at the same site respect to the initial capture site, other individual recaptured twice at the same site respect to the initial capture site, and another individual recaptured once at a different site respect to the initial capture site.

OOPHAGA PUMILIO DIET

The diet of this species consisted of 17 types of prey (Table 1) and was dominated numerically by acarines (43.9 %), Formicids (38.1 %) and collembolans (9.6%). Volumetrically, the diet was composed mainly for polydesmidans and coleopterans (26.6% and 15.8%, respectively). The most frequently prey were formicids and acarines, (87.5% of adults), and collembolans (67.5% of adults). Considering IPS the most important prey were acarines, formicids, collembolans and coleopterans (Figure 2). Prey diversity was 1.33 and niche breath of prey and prey volume was 2.86 and 7.57 respectively. The mean of body length and mouth was 20.41 ± 1.06 mm, and 6.23 ± 0.42 mm, respectively. Mean Ln prey volume was not correlated with Ln mouth width ($r = -0.21$; $n = 40$; $P = 0.19$). The proportions of microhabitats used were: (1) wet ground covered with ferns (17.5%), (2) leaf litter associated with the base of cacao plants and trees (82.5%), (3) associated with ant nests (0%), (4) under fallen trunks (0%).

DENDROBATES AURATUS DIET

This anuran consumed 14 prey categories (Table 1), being formicids (69.01 %), acarines (20.8 %), and collembolans (5.9%) dominant prey in number. Volumetrically, the diet was dominated by zorapterans and dermapterans (22.5 % and 14.7 %, respectively). The most frequently prey were formicids (92.5% of adults) acarines (85% of adults) and collembolans (60% of adults). Considering IPS the most important prey were, formicids, acarines, collembolans and coleopterans (Figure 2). Prey diversity was 0.96 and niche breath of prey item and prey volume was 1.90 and 8.09, respectively. The mean body length and mouth were 25.36 ± 4.25 mm and 7.47 ± 1.25 mm, respectively. Mean Ln prey volume was not correlated with mouth width ($r = -0.05$; $n = 40$; $P = 0.73$). The proportions of microhabitats uses were: (1) wet ground covered with ferns (55%), (2) leaf litter associated with the base of cacao plants and trees (12.5%), (3) associated with ant nests (17.5%), (4) under fallen trunks (15%).

Trophic and microhabitat overlaps. Considering prey proportion between the two dendrobatids the trophic niche overlap was high ($O_{jk} = 0.87$). Random-

izations with all data produced no significant difference between measured (observed) and simulated (expected) overlaps using diet proportion (P [observed < expected] = 0.83, and P [observed > expected] = 0.16). Therefore, observed mean (0.75) was similar to that expected by chance (0.73 ± 0.019). Moreover prey volumes were highly overlaped (O_{jk} = 0.76). Randomizations with all data produced no significant differences between measured (observed) overlaps and simulated (expected) prey volume overlaps (P [observed < expected] = 0.82, and P [observed > expected] = 0.18). Consequently, the observed mean (0.76) was similar to that expected by chance (0.75 ± 0.016).

The spatial niche overlap between the two frog species was low (Oj_k = 0.38). Randomizations with microhabitat data produced no significant differences between measured (observed) and simulated (expected) (P [observed < expected] = 0.51, and P [observed > expected] = 0.48) overlaps. The observed mean (0.38) was similar to that expected by chance alone (0.47 ± 0.06).

DISCUSSION

We found similarities in prey categories and diet composition between *D. aurautus* and *O. pumilio* (in term of number and frequency importance: formicids, acarines and collembolans). The IPS reflects the four same prey items for both dendrobatids, differing only in the order of the two most important prey item. Thus, in *D. aurautus* formicids were most important prey than acarines, while in *O. pumulio* it was the opposite. The values of niche breadth of prey volume for both dendrobatids were wider to those reported by Caldwell (1996). It may be due to the consumption of prey with great volume such as dermapterans, and polydesmidans, recorded in *D. auratus* and, such as polydesmidans and isopods recorded in *O. pumilio* in this study, but absent in Caldwell (1996). However, the proportions and frequency of these prey were very low in both dendrobatids, respectively. In fact its diets were predominantly characterized for the consumption of smaller prey, as was reflected in the lack of correlation between the volume of prey and the widths of the mouths of predators suggesting that both species select small prey. According to Caldwell (1996), *D. auratus* and *O. pumilio* eat mainly on smaller prey like ants and mites, who reach a length mean of 2 and 0.6 mm, respectively.

Considering only the prey type, *D. auratus* and *O. pumilio* appears to be as generalist predators, because these animals consumed a wide variety of prey. However, the prey type proportions consumed by this species showed that they are specialist on formicids and acarines. The proportionately higher number of fomicids and acarines in the *D. auratus* and *O. pumilio* diet resulted in a constricted niche breadth and in a low diversity index in both species. These results are consistent with the results of previous studies (Liberman, 1986; Donnelly, 1991; Caldwell, 1996). Constricted niche breadth suggests an actively foraging strategy (Perry and Pianka, 1997), which has been suggested for *D. auratus* and *O. pumilio* (Toft ,1981; Taigen and Pough, 1983). However predators that are specialist in colonial insects are active when they need to encounter the colony. After that, the predator can act as a sit-and-wait predator (Pianka, 1973; Donelly, 1991; Duré and Kehr, 2004). In fact, some *D. auratus* (recaptures not considered in the analysis) were observed returning each day to the same anthill and forage on this, as were also documented by Pough and Taigen (1990). Thus, considering the great proportion of formicids in the *D. auratus* and *O. pumilio* diets and in agreement with previous observations (Donnelly, 1991) the foraging strategy employed by this species can be consid-

ered intermediate between a sit-and-wait and active predator.

Individuals of *Dendrobates auratus* were registered in microhabitats mainly characterized by high moisture and low sun exposure, as wet ground covered with ferns, the microhabitat more frequently used. On the other hand, individuals of *O. pumilio* were found mostly in the leaf litter associated with the base of cacao plants, a microhabitat with lower moisture and higher degree of sun exposure. These microhabitats observations, are consistent with the reports made by Kitasako (1967) and Guyer and Donnelly (2005) which observed a humid and shaded microhabitat preference in *D. aurautus*, such as leaf litter associated with nooks and crevices offered by buttresses of trees and fallen trunks, and observed a preference for fairly sunny exposed microhabitats in *O. pumilio*, such as leaf litter at the base of cacao plants. We not found *O. pumilio* in association with fallen trunks or prey nests (e.g. anthills). However Kitasako (1967) and Donnelly (1991), report the occasional use of these microhabitats in *O. pumilio*.

Niche breadth of prey proportion and prey volume for the two species overlapped extensively (O_{jk} = 0.75; O_{jk} = 0.76, respectively) indicating a similarity between the diets. However the overlapping for each case was not significant. Thus, the overlap in diets does not imply a negative interaction between *D. auratus* and *O. pumilio*. The spatial niche overlap between the two dendrobatids was low (O_{jk} = 0.38) and no significant, indicating a differentiation on use of spatial resource. The traditional opposite interpretation of a high overlap indicates shared resource utilization and a lack of competition (Gotelli and Graves, 1996), or a strong competition that has not yet led to divergence in resource use (Connell, 1980; Sale, 1974). In summary, despite the fact that *D. auratus* and *O. pumilio* had a high trophic niche overlap, our results suggest that differences in microhabitat utilization seem to be an important factor favoring the absence of negative feeding interactions and consequently the coexistence between *D. auratus* and *O. pumilio* at the study site. Differentiation in space use was indicated by Cunha and Vieira (2004) as a mechanism that might counteract complete overlap in diet. An optional interpretation of the high overlap in trophic niche, without implying a negative interaction could be explained by an abundance of resources in the area sufficient to satisfy demands. Donnelly (1991) remarked that the inclusion of prey other than ants or mites in *O. pumilio* indicates that frogs respond to naturally occurring fluctuations in prey population sizes by consuming a variety of prey types.

The niche complementarity hypothesis states that for coexistence to occur, high overlap in one dimension of the niche must be compensated by low overlap in another (Schoener 1974). Our results suggest that in the period of our study, *D. auratus* and *O. pumilio* exhibit niche complementarity, with a high overlap in diet but low overlap in feeding microhabitat. However, as were pointed out above, *D. auratus* and *O. pumilio* occurs sympatrically at many sites along its distribution, but at La Selva this condition is not natural. Thus, our results are not extrapolated to a real sympatric situation but represents valuables ecological observations where the introduction of *D. auratus* must be evaluated at light of negative possible effects on the ecology of the resident frog *O. pumilio*. Further integrated diet studies that include sex, ontogeny, seasonality, microhabitat use, daily activity, prey availability and interactions are needed to better understand the interspecific relationships and coexistence between these two dendrobatids species at La Selva.

Dendrobatids, and members of other three anuran family (Mantellidae, Bu-

fonidae and Myobatrachidae), are known as poison frogs by the presence of alkaloids in dermal skin glands, which act as chemical defense against predators and/or microorganism. Indeed, more than 800 alkaloids, organized into 23 structural classes, were reported from the skin of poison frogs mentioned above (Saporito *et al*., 2009). The presence of alkaloids in poison frogs was attributed to the three process: 1) biosynthesis, where the frogs synthesize the alkaloids, 2) sequestration, where the frog sequesters the alkaloids from a food source and incorporate at its dermal glands, and 3) sequestration and *de novo* biosynthesis, where the frog sequester an alkaloid from a food source an use it then to synthesize a new alkaloid (Saporito *et al*., 2009). Several dendrobatids species are also known as ant and mite specialist (Toft, 1980a, Donnelly, 1991; Caldwell, 1996), and experimental evidence indicate that diet specialization in poison frogs is closely related to presence of alkaloids in dermal skin glands. Certainly, the analysis of skin extracts of some dendrobatids specimens raised in captivity and fed with fruit flies (*Drosophila* sp.) showed an absence of alkaloids in its skins, while specimens provided with fresh leaf-litter from the frog's natural habitat, accumulated a variety of alkaloids into the skin. In addition, the simultaneous occurrence of several structural classes of alkaloids present in arthropods from the frog´s natural habitat and the frog skin extracts reinforce the hypothesis of a dietary source of alkaloids (Daly *et al*., 2000). Recent studies conducted in dendrobatids frogs, indicate that principally ants and oribatid mites, and secondarily coleopterans and millipedes, represents a dietary sources of alkaloids (Saporito *et al*., 2003; Saporito *et al*., 2004; Saporito *et al*., 2007). Representatives of many of the structural classes of alkaloids, such as pumiliotoxins, decahydroquinilines, izidines, spiropyrrolizidines, have been detected in skin extracts of *D. aurautus* y *O. pumilio*, and also in ants, mites and millipedes consumed by this frogs. The great volume, frequency of occurrence and number of ants and mites reported in the present study for *D. auratus* and *O. pumilio*, is consistent with the hypothesis of arthropods as a dietary source of alkaloids.

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